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LETTER TO THE EDITOR

Space dimension and scaling in fish school-size distributionsEric Bonabeau^{||}, Laurent Dagorn^{‡¶} and Pierre Fréon^{§+}[†] Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, NM 87501, USA[‡] Orstom, BP 259, Papeete, French Polynesia[§] Orstom, BP 5045, 34032 Montpellier Cédex 1, France

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Abstract. A simple model of aggregation has been used, in its mean-field version, to explain the observed scaling property of tuna fish school-size distributions (Bonabeau E and Dagorn L 1995 *Phys. Rev. E* **51** 5220). This model makes additional predictions when the dimension of the space in which the fish move is taken into account. In this letter, we identify two cases where the mean-field assumption, which was justified for free-swimming tuna fish, is no longer valid. In these two examples, scaling is also observed and the exponent is modified from the mean-field case in a way predicted by the model.

Grouping is a widespread phenomenon throughout the animal kingdom, that has been modelled both by biologists [1–5] and physicists [6, 7]. Groups may be more or less stable [1]. The stability or lack of stability of groups influences the properties of group-size distributions: species with unstable groups should be characterized by rapidly decreasing distributions, whereas species with stable groups may in principle be characterized by long-tailed distributions if there is a sufficiently large reservoir of individuals. Animal group-size distributions [1–4] have been extensively studied, but the possibility of scaling [7] in such distributions has been overlooked. There are several possible reasons for this. First, power-law distributions $N(s) \propto s^{-b}$, where $N(s)$ is the observed number of groups of size s , and b the power-law index, do not have a well-defined mean when $b \leq 2$ —a property that may appear non-biological. Second, in his influential review, Okubo [1] determined that any group-size distribution should be exponentially decreasing. He did this by applying a maximum entropy principle to the distribution, under the constraint of fixed average size, which implicitly includes the strong assumption that there exists a well-defined mean, and it is well known to physicists that such a procedure leads to exponential distributions. Third, long-tailed group-size distributions are necessarily truncated at a cut-off size because the population is finite, and are ultimately rapidly decreasing for very large sizes, but truncated power laws must be distinguished from purely rapidly decreasing ones. For example, sums of power-law distributed random variables exhibit hyperslow convergence to the normal distribution [8]. Note that the existence of a cut-off size implies that there eventually exists

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an average size, even for $b \leq 2$, but that this average size is very different from the *typical* size.

If the possibility of power laws in animal group-size distributions has been overlooked by biologists, scaling has been known to be present in cluster-size distributions obtained from physical models of aggregation–fragmentation [9, 10]. Motivated by the observation of power-law size distributions with an index close to $b = 1.5$ in tropical tuna fish schools [7], we have previously proposed a simple mean-field model of aggregation [7, 9], arguably the simplest possible model, to account for the observation: namely, that fish schools be considered as particles that move between sites and aggregate when they meet. Let us briefly sketch how the exponent $b = 1.5$ is obtained. We assume that the simulated fish can hop from site to site and that m fish swimming together form an m -school. At each discrete time step, all schools move towards a randomly selected site (all N sites are selected with equal probability). When an m -school and an h -school hop to the same site, they aggregate to form an $(m + h)$ -school. When fish are regularly injected into the system, this simple aggregation process leads to a stationary power-law distribution. Let us introduce the characteristic function $Z_1(\rho, t)$ of the size distribution $D(s)$ at time t , $Z_1(\rho, t) \equiv \langle \exp[i\rho s] \rangle$, where $\langle \dots \rangle$ denotes the average over all possible realizations of the aggregation process. We obtain $Z_1(\rho, t + 1) = \Phi(\rho)e^{Z_1(\rho, t)-1}$, where $\Phi(\rho)$ is the characteristic function of the injection random variable I . Each site has a different realization of the same injection variable I . The detailed derivation can be found in [7, 9]. $\Phi(\rho)$ can be expanded as $\Phi(\rho) = 1 + i\langle I \rangle \rho - (\langle I^2 \rangle \rho^2 / 2) + \dots$, where $\langle I \rangle$ and $\langle I^2 \rangle$ are the first two moments of I . In the stationary state, $Z_1(\rho)$ satisfies $Z_1(\rho) = \Phi(\rho)e^{Z_1(\rho)-1}$. Taking the limit $N \rightarrow \infty$, one obtains the steady-state characteristic function $Z_1(\rho) = 1 - \sqrt{2}\langle I \rangle^{1/2}|\rho|^{1/2}i^{-1/2} + \dots$, so that the size distribution satisfies $D(s) \propto s^{-3/2}$ for large enough s ($s \gg \langle I \rangle$). Figure 1 shows the number of aggregates $N(s)$ of size s obtained from a simulation in which one new size-one individual is injected into the system at every time step.

If the injection process is replaced by school-splitting and the reinjection of individuals that have left their schools, while keeping the total number of individuals fixed, one obtains a truncated power law with the same exponent, up to a cut-off size that depends, among other things, on the timescale of splitting [7]. To see how a cut-off size appears, let us assume that n is constant over time, that a fraction p of each group is separated from the group at every time step, and that the corresponding pn individuals are reinjected by being randomly redistributed among the N sites. The expectation of the injection is pn/N . The characteristic function is now given by $Z_1(\rho, t + 1) = \Phi((1 - p)\rho)e^{Z_1((1 - p)\rho, t)-1}$, so that $Z_1(\rho) = 1 - i\langle s' \rangle \rho + \dots$: the size distribution is short-ranged with a finite mean $\langle s' \rangle = (1 - p)n/N$. Although the size distribution now has a characteristic scale, it retains its power-law characteristics up to the cut-off size, as can be seen on figure 2. Figure 2 also shows the size distribution of schools of freely swimming tuna fish (in which three species, yellowfin tuna *Thunnus albacares*, skipjack tuna *Katsuwonus pelamis*, and bigeye tuna *Thunnus obesus* are mixed) [7]. The similarity between the empirical distribution and the distribution obtained from the model is striking. In order to fit the empirical distribution, we examine fitting functions of the type $N(s) \propto as^{-b}f(s/s_c)$, with $f(x) = e^{-x^c}$, where a , b , c and s_c are four fitting parameters and f is a crossover function from power-law to exponential decay. For simplicity, we restrict our attention to $1 \leq c \leq 2$. We find that the best fit is given by $a = 3497$, $b = 1.49$, $c = 2$, $s_c = 29.7$ for free tuna (dotted curve in figure 2). The b exponent, $b = 1.49$, is quite close to the mean-field prediction $b = 1.5$.

This model not only produces a power-law index $b = \frac{3}{2}$ in its mean-field version [7, 9], in which schools can move from any site to any other site; it also generates several predictions which may be important for our understanding of fish schools. For example, depending on

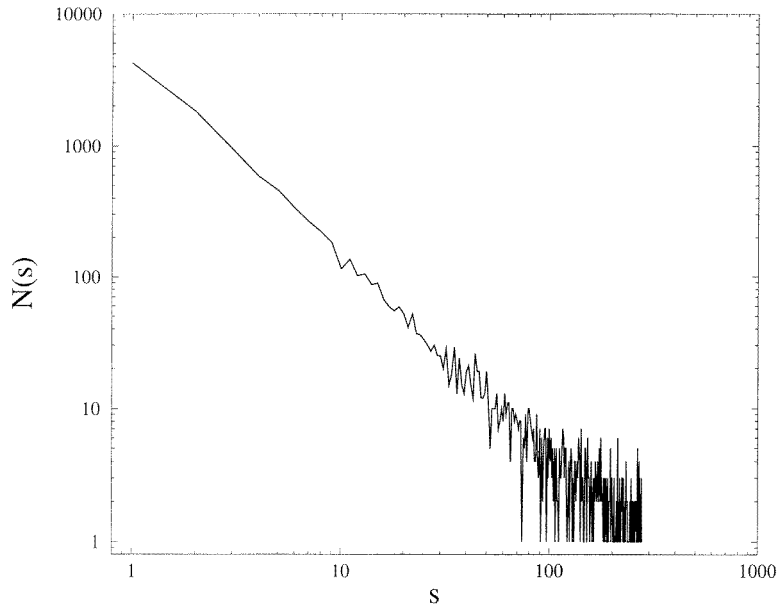


Figure 1. Log–log plot of $N(s)$ versus s , where $N(s)$ is the number of aggregates of size s obtained in the mean-field simulation after 8×10^4 time steps. Simulation with $N = 100\,000$ sites. One individual of size one is injected into the system at a randomly selected site at each time step.

environmental conditions, the stability of groups of a given species may vary: for instance, the lack of food may reduce group stability [11]. If the group-size distribution is a power law, and if the model is relevant to explain the origin of the power law, then we expect such factors to affect the cut-off size but not necessarily the power index b [7]. The data obtained from catches by purse seiners is consistent with this prediction, since b is relatively robust over the years while the cut-off size varies [7]. This indicates that the overall shape of the distribution may result from a simple underlying aggregation mechanism, whereas the cut-off size results from fluctuating environmental conditions or variable individual behaviour. It is tempting to think that the model does explain the origin of the observed power-law distribution, all the more as it exhibits robust scaling (that is, scaling with a similar exponent) when various features are included [7, 9]. Notice, however, that although we use the model described in [9] (mostly because its simple formulation directly applies to our problem), other related models of coagulation–fragmentation, based on a Smoluchowski rate equation including a break-up kernel, are also available with comparable predictions [10].

Let us now examine additional predictions of the model related to the ‘effective’ dimension d of the space in which the fish move. By effective dimension, we mean that, although the ocean is three-dimensional, fish may not use the whole ocean and may, for instance, be constrained to swim along the coasts, or, alternatively, may move so quickly from one location to another that space is irrelevant. This latter constraint, which can, to a large extent, apply to freely swimming tuna fish, corresponds to the mean-field version of the aggregation model which leads to $b = \frac{3}{2}$ whereas the empirical distribution gives $b = 1.49$ (figure 2). The critical dimension of the model is between four and five [9]. An exact result can be obtained for $d = 1$: $b = \frac{4}{3}$. For other dimensions, simulations (the results of which are reported in [9]) indicate that $b = 1.465 \pm 0.003$ for $d = 2$; $b = 1.491 \pm 0.007$ for $d = 3$;

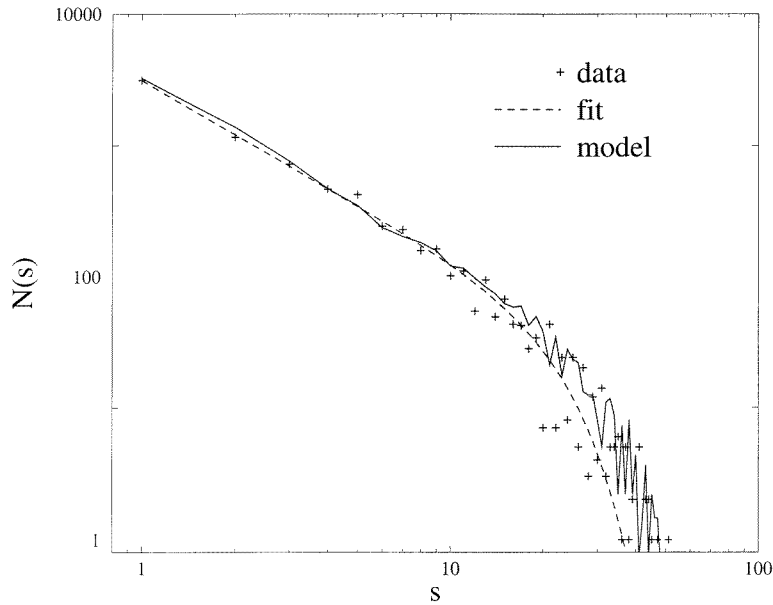


Figure 2. Crosses represent the school-size distribution of free swimming tuna fish (yellowfin tuna, skipjack tuna, bigeye tuna). The dotted curve corresponds to a fit of the type $as^{-b}e^{-(s/s_c)^c}$, with $a = 3497$, $b = 1.49$, $c = 2$, $s_c = 29.7$. The full curve has been obtained from simulation of the mean-field model after 10^6 time steps, with $N = 100\,000$ sites, $n = 80\,000$ individuals, $p = 0.1$. All individuals are initially present and randomly distributed among sites.

and $b = 1.496 \pm 0.010$ for $d = 4$. As a general trend, b increases when d increases for $d < 5$. Therefore, we expect species for which the effective dimension is less than three to be characterized by $b < \frac{3}{2}$.

We have identified two cases in which the effective dimension may be less than three: (1) tuna fish in the presence of a fish aggregating device (FAD), which can be a drifting log or an artificial device designed to attract fish, and (2) some species of sardinellas (family of sardines—*Sardinella maderensis* and *Sardinella aurita*), which do not make full use of the three-dimensional oceanic space. In example (1) it can be argued that the effective dimension is less than one because the FAD is a point. In example (2) the effective dimension lies between one and two because sardinellas tend to swim along the coast (at a distance limited to at most 10 times the width of the continental plateau)—which reduces the effective dimension by one—where water depth is smaller than far from the coast, which further reduces the effective dimension by an unknown factor. Figures 3 and 4 show the school-size distributions of, respectively, tuna fish caught in the vicinity of a FAD [12] (figure 3) and sardinellas caught in the up-welling areas of the west African coast (figure 4). The best fits (of the type $as^{-b}e^{-(s/s_c)^c}$, $c = 1, 2$) are also represented for these distributions:

- $a = 1113.3$, $b = 0.698$, $c = 1$, $s_c = 3.72$ for tuna caught in the vicinity of a FAD (figure 3),

- $a = 503$, $b = 0.95$, $c = 2$, $s_c = 59.8$ for sardinellas (figure 4).

We observe that, although the exponents b are not exactly those of the model, there is a clear decrease of b with effective space dimension ($b = 1.49$ for freely swimming tuna fish, $b = 0.95$ for sardinellas, and $b = 0.698$ for tuna fish caught in the vicinity of a FAD), consistent with the model's general prediction. So, despite several factors that

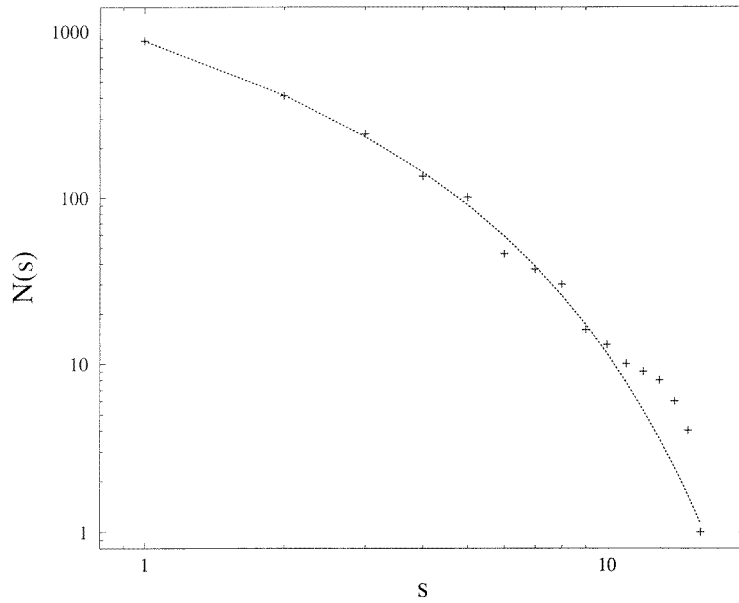


Figure 3. School-size distribution of tuna fish caught in the vicinity of a FAD. The dotted curve corresponds to a fit of the type $as^{-b}e^{-(s/s_c)^c}$, with $a = 1113.3$, $b = 0.698$, $c = 1$, $s_c = 3.72$.

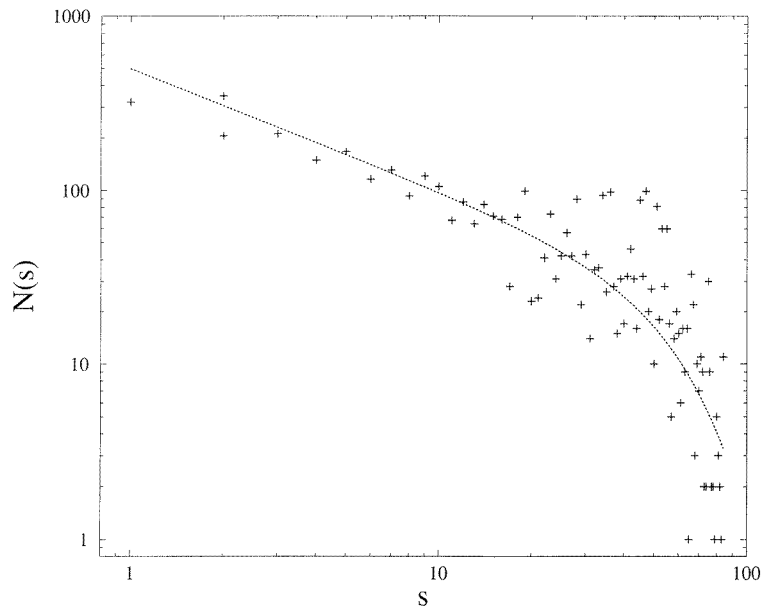


Figure 4. School-size distribution of sardinellas caught in the up-welling areas of the west African coast. The dotted curve corresponds to a fit of the type $as^{-b}e^{-(s/s_c)^c}$, with $a = 503$, $b = 0.95$, $c = 2$, $s_c = 59.8$.

many bias school-size estimates (the whole school is not always caught, especially if it is large; fishermen sometimes do not wish to catch small schools; several species are often mixed in schools; and school sizes are measured by weight not number) and despite the

lack of accurate quantitative estimates of dimensional reduction, the remarkable consistency between these results and the model's prediction is strong evidence that the simple model of aggregation contains some of the essential ingredients of fish schooling behaviour that influence school size. Moreover, the reported $b = 1.2$ exponent for herds of the African buffalo (*Syncerus caffer*) [7, 13], whose movements take place in a two-dimensional space, reinforces this interpretation and suggests that the model can apply to terrestrial animals as well.

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